Department für Kleintiere, Klinik für Zoo-, Heim- und Wildtiere

der Vetsuisse-Fakultät Universität Zürich

Direktor: Prof. Dr. Jean-Michel Hatt

Arbeit unter Leitung von PD Dr. Marcus Clauss

Variation in growth of herbivorous tortoises: causes and consequences for reproduction and health management

Inaugural-Dissertation

zur Erlangung der Doktorwürde der

Vetsuisse-Fakultät Universität Zürich

vorgelegt von

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Tierärztin

von Hüntwangen, ZH

genehmigt auf Antrag von

PD Dr. Marcus Clauss

Zürich 2011

Inhaltsverzeichnis

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Variation in growth of herbivorous tortoises: causes and consequences for reproduction and health management

Reptiles have very flexible growth rates, depending on living conditions - in particular dietary resources. Here, I demonstrate a difference in the growth rates of captive specimens, as compared to literature data for free-ranging ones, in Leopard tortoises (*Geochelone pardalis*), African spurred tortoises (*G. sulcata*), Hermann's tortoises (*Testudo hermanni*) and Spur-thighed tortoises (*T. graeca*). Such high growth rates are traditionally thought to be linked to health problems. In the case of the *G. sulcata* dataset (spanning 18 years for the captive individuals), it could be shown that fast growth leads to a fast reproductive maturity, as expected from inflexion points of growth curves. In a retrospective evaluation of 539 tortoise patients of the University of Zurich, no evidence for diet- or growth-related disease risk was found in animals that were particularly heavy for their age. However, typical diet- or growth-related disorders were more frequent among younger patients, suggesting that animals with such problems do not often survive to older age. Raising tortoises on intensive feeding regimes in captivity may considerably shorten generation times during the breeding stage of restocking programmes. Whether fast growth presents a health risk needs to be evaluated in controlled studies. The observations also suggest that feeding regimes in captivity – even of appropriate diets - should be restricted if replication of conditions in the wild is a husbandry objective.

Key words: tortoise, growth, feeding, reproduction, health, pyramiding

Variation im Wachstum herbivorer Schildkröten: Auslöser und Konsequenzen für Fortpflanzung und Gesundheitsmanagement

Reptilien haben sehr flexible Wachstumsraten, je nach Haltungsbedingungen – insbesondere je nach Fütterung. Hier werden Unterschiede im Wachstum bei Individuen aus Menschenobhut und freier Wildbahn belegt für Panther- (*Geochelone pardalis*), Sporen- (*G. sulcata*), Griechische (*Testudo hermanni*) und Maurische (*T. graeca*) Landschildkröten. Solche hohen Wachstumsraten werden traditionell als Gesundheitsproblem betrachtet. Im Falle des 18 Jahre umfassenden Datensatzes zu *G. sulcata* konnte gezeigt werden, dass ein schnelles Wachstum zu einer raschen sexuellen Reife führt, so wie man es aufgrund des Umkehrpunktes der Wachstumskurve erwartet. Bei einer retrospektiven Auswertung von 539 Schildkröten-Patienten der Universität Zürich wurde kein Hinweis dafür gefunden, dass für ihr Alter schwere Tiere eher zu fütterungs- oder wachstumsbedingten Problemen neigen. Solche Probleme traten aber häufiger bei jüngeren Tieren auf, was darauf hinweisen könnte, dass Tiere mit solchen Problemen nicht alt werden. Schildkröten intensiv zu füttern könnte eine Strategie sein, um die Generationszeiten in Nachzuchtprogrammen zu verkürzen. Ob hohe Wachstumsraten wirklich die Gesundheit gefährden, muss in kontrollierten klinischen Studien untersucht werden. Die Ergebnisse legen nahe, dass man Schildkröten – auch mit adäquaten Futterrationen – restriktiv füttern muss, wenn man die Bedingungen in freier Wildbahn imitieren will.

Schlüsselworte: Schildkröte, Wachstum, Fütterung, Fortpflanzung, Gesundheit, Höckerbildung

meiner Familie gewidmet

Artikel 1

Zoo Biology 29 : 517–525 (2010)

TECHNICAL REPORT

Body Size Development of Captive and Free-Ranging Leopard Tortoises (*Geochelone pardalis*)

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The growth and weight development of Leopard tortoise hatchings (*Geochelone pardalis*) kept at the Al Wabra Wildlife Preservation (AWWP), Qatar, was observed for more than four years, and compared to data in literature for free-ranging animals on body weight or carapace measurements. The results document a distinctively faster growth in the captive animals. Indications for the same phenomenon in other tortoise species (Galapagos giant tortoises, *G. nigra*; Spur-thighed tortoises, *Testudo graeca*; Desert tortoises, *Gopherus agassizi*) were found in the literature. The cause of the high growth rate most likely is the constant provision with highly digestible food of low fiber content. Increased growth rates are suspected to have negative consequences such as obesity, high mortality, gastrointestinal illnesses, renal diseases, "pyramiding," fibrous osteodystrophy or metabolic bone disease. The apparently widespread occurrence of high growth rates in intensively managed tortoises underlines how easily ectothermic animals can be oversupplemented with nutrients. Zoo Biol 29:517–525, 2010. © 2009 Wiley-Liss, Inc.

Keywords: captive breeding; *Geochelone pardalis*; leopard tortoise; morphometrics; testudinae; tortoise growth

Grant sponsors: Gesellschaft Schweizer Tierärztinnen und Tierärzte; Schweizerische Vereinigung für Wild-, Zoo- und Heimtiermedizin.

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Received 9 January 2009; Accepted 15 June 2009

DOI 10.1002/zoo.20273
Published online 31 August 2009 in Wiley Online Library (wileyonlinelibrary.com).

INTRODUCTION

The Leopard tortoise [*Geochelone pardalis*, Bell, 1827], one of the largest mainland tortoise species, ranges from Eastern to Southern Africa [Iverson, 1992]. Despite its wide distribution, the knowledge about this species, particularly its growth and development, is limited. Available data from literature are primarily concerned with patterns of the body mass and the body size, correlating weight and length measurements in free ranging [Lambert, 1995; Lambert et al., 1998; Hailey and Coulson, 1999; Kabigumila, 2000, 2001] or captive specimens [Wilson, 1968; Rall, 1988]. Although such information emphasizes the consistency of these correlations, they offer little guideline for the husbandry of the species, because the most important question for raising tortoises—the correlation of body mass and age—cannot be addressed. The only study providing information about the body mass development with age in Leopard tortoises is by Wilson [1968], who kept animals in confinement but did either not offer food or just supplement some greens in addition to the natural vegetation. Additionally, Hailey and Coulson [1999] and Hailey and Lambert [2002] presented data on the total length of free-ranging Leopard tortoises in relation to age.

A growth rate exceeding that of natural populations is suspected to occur in many captive and pet tortoises, with potential pathological consequences such as obesity, high mortality, gastrointestinal illnesses, renal diseases, "pyramiding," fibrous osteodystrophy or metabolic bone disease [Häfeli and Schildger, 1995; McArthur, 2004a; McArthur and Barrows, 2004; Donoghue, 2006; Hatt, 2008]. On the one hand, empirical studies on the correlation of fast growth with any of these conditions are lacking; on the other hand, growth curves for natural or captive tortoises that relate age to other parameters are rare. This lack of guidelines induces a component of uncertainty in tortoise husbandry. To our knowledge, the only published data on a comparison of age-related growth in intensively kept and extensively kept, respectively free-ranging herbivorous land tortoise species are on Galapagos giant tortoises (*Geochleone nigra*) by Furrer et al. [2004] and on Spur-thighed tortoises (*Testudo graeca*) by Lapid et al. [2005].

In this contribution, we present data on the growth of Leopard tortoises kept at the Al Wabra Wildlife Preservation (AWWP), Doha, State of Qatar, and compare the data with the specimens managed by Wilson [1968] on natural vegetation only and to free-ranging individuals investigated by Hailey and Coulson [1999] and Hailey and Lambert [2002].

METHODS

Leopard tortoises have been kept at AWWP since 1999. Juveniles hatched each year from May to October (between 2002 and 2007). Animals were kept in enclosures with a natural vegetation of grasses and small shrubs with a regular supplement of a variety of vegetables (tomato, carrot, bell pepper, zucchini, cucumber and pumpkin), fruits (melon, papaya, grapes, apple, pear, berries, banana and cactus fruits), fresh lucerne (*Medicago sativa*), fresh grasses, browse (*Ziziphus spina-christis*), flowers and grass hay ad libitum. Absolute amounts ingested, and the nutritional composition of the diet, were unknown. Hatchings were repeatedly weighed and measured several times per year in varying intervals between 2002 and 2008 (age groups 2002–2006

consisting of 3–50 animals). The investigations included totally 109 Leopard tortoises. Fecal samples were taken regularly, most of the cases without parasite findings. In positive cases the treatment of choice was Fenbendazole (50 mg/kg) for 2 days every other week for 3 weeks or Prazinquantel (8 mg/kg) for 1 day every other week for 3 weeks. The animals included in this study were assessed until two to nearly four and a half years of age. Apart from body mass, measurements included the total length (straight carapace length), the plastron length and the height of the tortoises, measured by callipers (straight measurements) and the curved carapace length and width measured by a soft tape (curved measurements). Data were recorded to the nearest millimeter or the nearest gram, respectively.

RESULTS

The animals of all investigated age groups showed a regular allometric body form development similar to previously published patterns in the same species [Wilson, 1968; Rall, 1988; Lambert, 1995; Lambert et al., 1998] (Fig. 1). Therefore, the relationship of body proportions and body weight are consequently the same in the captive animals and in the free living or not artificially fed individuals.

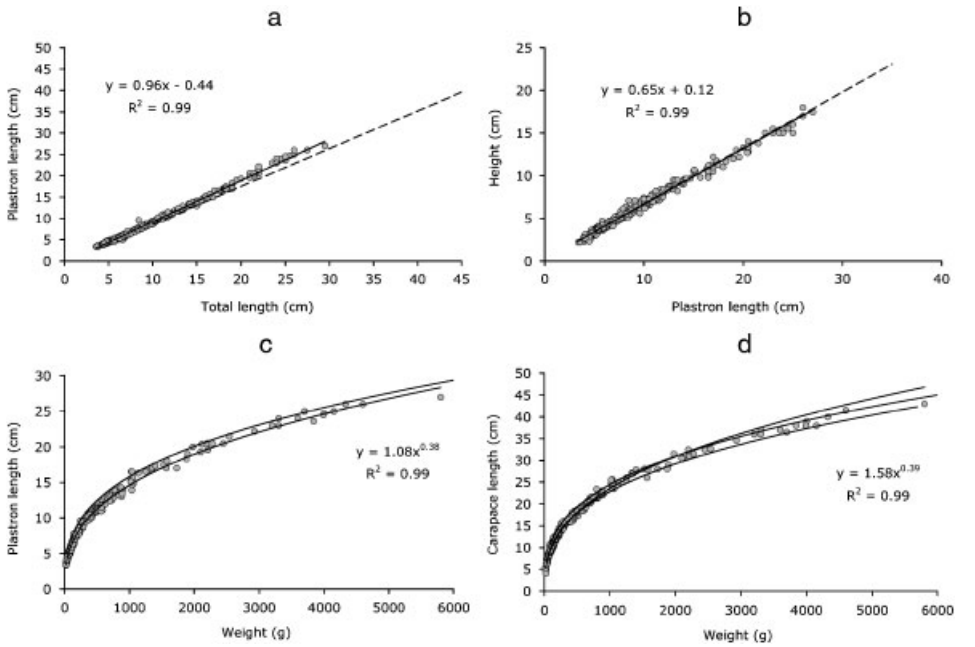

Fig. 1. The allometric relationship between (**a**) total length and plastron length from the Leopard tortoises (*Geochelone pardalis*) at AWWP (data points and solid line) compared to literature [Lambert, 1995, interrupted line, $y = 0.88x - 0.17$], (**b**) plastron length and height from the Leopard tortoises at AWWP (data points and solid line) compared to the data from Lambert et al. [1998, interrupted line, $y = 0.66x + 0.17$], (**c**) weight and plastron length from the Leopard tortoises at AWWP compared to the data from Wilson [1968, upper regression line, $y = 1.45x^{0.35}$] and (**d**) weight and carapace length from the Leopard tortoises at AWWP compared to literature [Wilson, 1968, middle regression line, $y = 2.31x^{0.34}$ and Rall, 1988, lower regression line, $y = 1.97x^{0.35}$].

Among the animals raised at AWWP, differences in the body weight development between the different year cohorts are evident (Fig. 2a). In particular, animals hatched in 2002 and one group of animals from 2003 showed a slower body weight increase than the other animals. No difference in husbandry conditions could be elucidated in retrospect to which this difference could be attributed.

When the growth patterns of Leopard tortoises from AWWP are compared with the data from Wilson [1968], Hailey and Coulson [1999] or Hailey and Lambert [2002], a distinctive difference is evident (Fig. 2b). The animals kept at AWWP grew much faster than all the other individuals studied.

DISCUSSION

The captive population of Leopard tortoises at AWWP showed a dramatically faster growth pattern than conspecifics from the wild or kept in natural enclosures with hardly any food supplementation (Fig. 2). In this respect, the data for this species reveal the same pattern that can also be found in other tortoise

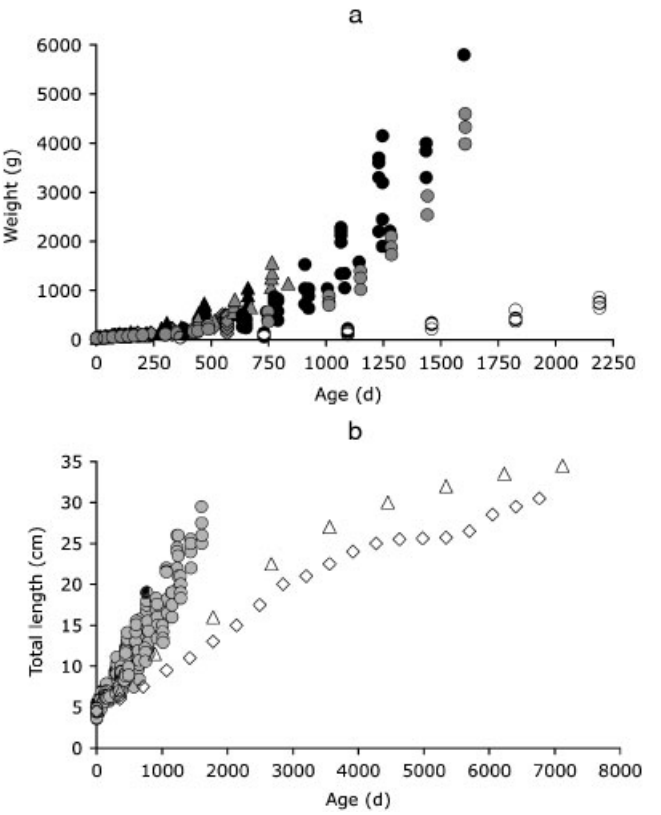

Fig. 2. Data showing (**a**) the weight development from the Leopard tortoises (*Geochelone pardalis*) at AWWP separated by birth years (2002 gray circles, 2003 black circles, 2004 gray triangles, 2005 black triangles, 2006 rhombs) compared with literature [Wilson, 1968, open circles] and (**b**) the growth of the total length from the Leopard tortoises at AWWP (gray circles) compared with literature [Hailey and Coulson, 1999, triangles; Hailey and Lambert, 2002, rhombs].

species—either in direct comparisons of captive and free-ranging populations, or when data from different publications are combined (Fig. 3). Free-ranging or extensively kept animals always grow much slower than intensively kept individuals.

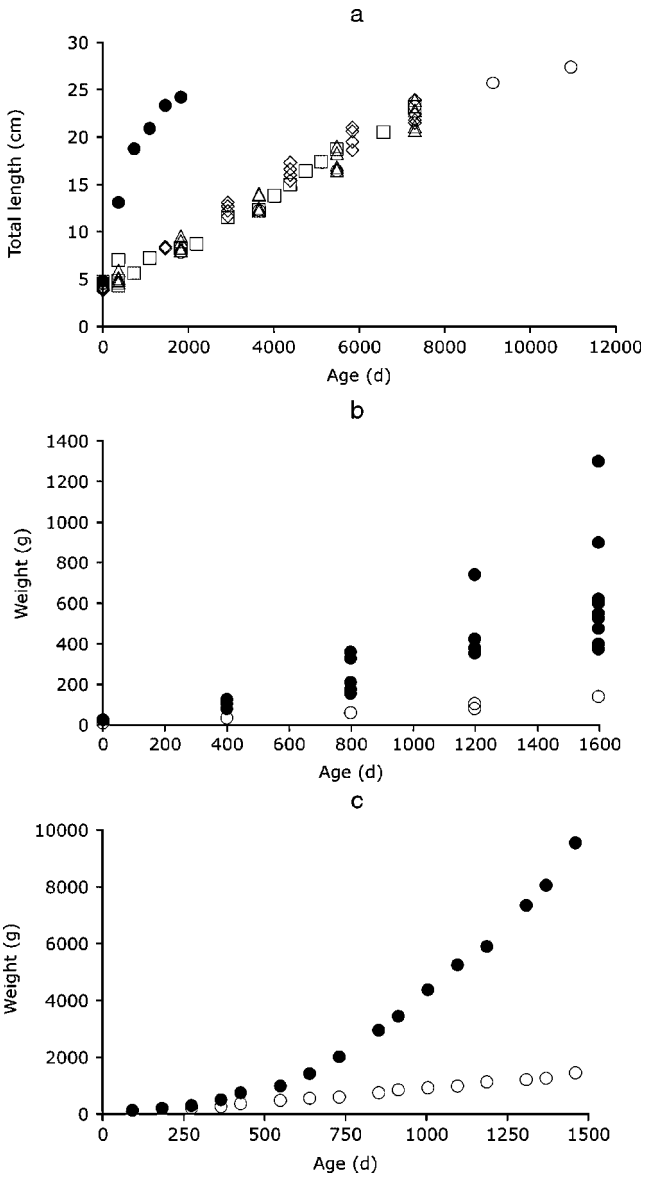

Fig. 3. Comparison of the different development of intensive and extensive nourished land tortoise species. (**a**) Age to total length of Desert tortoises (*Gopherus agassizi*) fed intensive [points, Jackson et al., 1976, 1978] and free-ranging [triangles, Germano, 1992; rhombs, Germano, 1994] or with a rather extensive feeding [squares, Miller, 1932, 1955; circles, Patterson and Brattstrom, 1972]. (**b**) Age to weight of captive Spur-thighed tortoises (*Testudo graeca*) fed with a high-energy diet (points) and free-ranging animals (circles) in Israel by Lapid et al. [2005]. (**c**) Age to weight of the Galapagos giant tortoises (*Geochelone nigra*) at the Zurich Zoo (points) and on Galapagos (circles), Furrer et al. [2004].

Similarly, McArthur [2004b] had presented qualitative evidence, in the form of photographs of two similar-aged Leopard tortoises from the wild and from captivity, respectively, that documented a faster growth in the captive individual.

In tortoises, growth patterns can be influenced by sexual dimorphism, or by environmental conditions. Growth patterns also vary between different populations of free-ranging individuals, most likely due to differences in habitat quality [Aresco and Guyer, 1999]. In the case of the Leopard tortoise, conflicting results have been published with respect to sexual dimorphism—some studies found sexual dimorphism in the species, with females being larger [Lambert et al., 1998; Kabigumila, 2000, 2001; Mason et al., 2000], but another study did not find evidence for it [Lambert, 1995]. The discrepancy is most likely explained by differences in environmental conditions between the study populations, because Hailey and Coulson [1999] noted differences in the degree of sexual dimorphism in Leopard tortoises between various geographic areas. Lambert et al. [1998] also remarked that growth varied geographically, probably due to environmental conditions such as differences in climate, bushfire incidence and predation pressure. For example, wet summers may increase activity and stimulate a higher food intake which leads to faster growth, whereas lower temperatures in winter reduce the activity, may even cause a hibernation, and thus slow down growth [Lambert, 1995]. Of course, these seasonal influences also have an effect on quality and abundance of food. The variation observed in the growth patterns between hatchling cohorts at AWWP is most likely explained by such (unnoticed) changes in environmental conditions.

Regardless of these factors that can influence a tortoise's development, the differences between intensively kept and free-ranging/extensively kept animals (Figs. 2 and 3) are of a dramatically higher magnitude than differences found in the wild due to environmental conditions or sexual dimorphism. In these cases, it seems obvious that the different living conditions of the populations—particularly the food offered to them—influence the growth considerably. Although direct experimental evidence for this assumption is mostly lacking, other authors also contributed the difference in growth between intensively kept and free-ranging/extensively kept animals to the feeding regime [Jackson et al., 1976, 1978; Furrer et al., 2004; Lapid et al., 2005]. To our knowledge, the only study that provided controlled evidence for an influence of the diet on growth in tortoises is the one by Fledelius et al. [2005], who investigated the influence of calcium supplementation on growth rates in Leopard tortoises. The animals with a daily calcium dose three times higher than recommended had the highest growth rate, whereas individuals receiving less calcium grew slower. A similar effect was reported in soft-shelled turtles [Huang et al., 2003]. In other reptiles, differences in growth rate due to differences in the provision with energy and nutrients have been described repeatedly [Statoh et al., 1990; Donoghue, 1994; Baer et al., 1997; Donoghue et al., 1998; Madsen and Shine, 2000; Rich and Talent, 2008]. These reports document a considerable potential of reptiles to accelerate or decelerate growth in reaction to the supply of food; we can only presume that this plasticity is more pronounced than in the case of the endotherm mammals or birds in which growth rates are probably less flexible. The combination of small initial body size, dramatically lower energy and nutrient requirements in ectotherms as compared with endotherms, lack of an increase in metabolic rate in growing as compared with adult tortoises [Brown et al., 2005], availability of food in captivity, and habituation to feeding (and consuming) amounts adequate for

endotherm maintenance on the side of animal keepers, makes an oversupplementation of food to tortoises likely whenever no special attention is paid to restrict this amount.

In addition to differences in the feeding regime, differences in the load of pathogenes and/or commensals, in particular gastrointestinal parasites, might play a role. In free-ranging tortoises, a variety of parasites have been reported [Jacobson, 1994] that will potentially reduce the amount of energy and nutrients available for growth in their hosts. Standard veterinary care for captive individuals, such as the regular parasitic control and treatment in the Leopard tortoises used in this study, could thus also contribute to faster development. To our knowledge, however, this has not yet been investigated in controlled studies.

Whether faster growth rates are actually linked to health problems can, so far, only be speculated upon. Although there appears to be a consensus in this respect in the reptile literature (see Introduction), experimental evidence is lacking. On an anecdotal level, Jackson et al. [1976, 1978] observed not only a dramatically faster growth in their intensively kept Desert tortoises as compared with free-ranging specimens (Fig. 3), but also noted that their animals showed a pyramiding growth pattern. Pyramiding has, so far not been observed in the Leopard tortoises at AWWP. In order to reduce the growth rate of hatchings at AWWP, and presumably contribute to a higher health standard of the following hatching cohorts, vegetables and fruits were excluded as a result of this study at AWWP, so that the current diet only includes the natural enclosure vegetation of grasses and shrubs, and additionally offered grass and lucerne hays. Future years will show whether this change in diet regime will reduce the growth rate of AWWP Leopard tortoises to levels reported in free-ranging specimens.

CONCLUSIONS

1. Intensively managed Leopard tortoise hatchlings showed a faster growth rate (as assessed by the development of body weight or body length over time) as compared with free-ranging or extensively kept specimens.
2. Similar observations were reported in the literature for Spur-thighed tortoises (*T. graeca*), Galapagos giant tortoises (*G. nigra*), and can also be made when comparing literature data on the growth of free-ranging and captive Desert tortoises (*G. agassizi*).
3. The literature reports on the influence of feeding on growth in reptiles make an intensive dietary supplementation in captivity the most likely explanation for this effect.
4. Although experimental evidence for a negative effect of fast growth on health of tortoises or reptiles is lacking, these observations suggest that in order to mimick conditions in the wild, feeding regimes in captivity should be restricted.

ACKNOWLEDGMENTS

This project was carried out as part of the Zoo Research Camp (ZRC) 2008, organized by AWWP and the Clinic for Zoo Animals, Exotic Pets and Wildlife of the Vetsuisse Faculty, Zurich. The authors thank Sheik Saoud Mohamed Bin Ali

Al-Thani for his support of the ZRC, as well as the "Gesellschaft Schweizer Tierärztinnen und Tierärzte" and the "Schweizerische Vereinigung für Wild-, Zoo- und Heimtiermedizin" for additional financial aid and Dr. Sven Hammer, Dr. Amrita Deb and the assistants to the mammal curator at AWWP for helping with measuring the tortoises and answering all our questions, and Professor Jean-Michel Hatt for comments on the manuscript.

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Artikel 2

Body size development of captive and free-ranging African spurred tortoises (*Geochelone sulcata*): high plasticity in reptilian growth rates

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In captivity, tortoises often grow faster than their conspecifics in the wild. Here, we document growth (measured as change in body mass) in three individual *Geochelone sulcata* over an exceptionally long period of nearly 18 years and use growth data (measured as change in carapace length) from the literature on free-ranging animals for comparison. Body lengths almost reached a plateau in the animals due to the long observation period. After transformation of body length to body mass for data from wild animals, logistic growth curves were successfully fitted to all data. The resulting functions yielded a 1.4–2.6 times higher intrinsic growth rate in captive than in wild individuals. The logistic growth model estimated the inflexion point of the growth curve at 6–9 years for the captive animals. This coincided with age at sexual maturity, respectively observations of first egg-laying of a female and the masturbation of a male. The inflexion point of the growth curve for free-ranging individuals was estimated at 15 years. Raising tortoises on intensive feeding regimes in captivity may considerably shorten generation times during the breeding stage of restocking programmes, and slow-growing animals are more likely to thrive after release into the wild. Investigations on the health of offspring from fast-growing parents are lacking.

Key words: ectotherm, body mass, body length, diet, conservation

Among breeders, it is well known that captive tortoises often show growth rates exceeding those of animals in the wild. Nevertheless, literature providing evidence for this assumption is rare. An excessive growth rate is suspected to lead to pathological consequences such as obesity, high mortality, gastrointestinal illnesses, renal diseases, "pyramiding", fibrous osteodystrophy, metabolic bone disease or dystocia (Lambert et al., 1988; Häfeli & Schildger, 1995; McArthur, 2004; McArthur & Barrows, 2004; Lapid et al., 2005; Donoghue, 2006; Hatt, 2008; Hänse et al., 2010). To our knowledge, age-related growth in captive/intensively kept versus free-ranging/extensively kept herbivorous tortoise species has so far been compared only for Greek tortoises (*Testudo hermanni*; Zwart et al., 1997), Galapagos giant tortoises (*Geochelone nigra*; Furrer et al., 2004), spur-thighed tortoises (*Testudo graeca*; Lapid et al., 2005) and leopard tortoises (*G. pardalis*; Ritz et al., 2010). Whenever such data were presented, it was for growing animals that had not been observed up to adulthood and cessation of growth; therefore, differences in growth rates and their consequences for the age at which sexual maturity was reached could not be reliably modelled. Despite the potential negative consequences of excessive growth, there may be one positive effect. Because sexual maturity is a function of body size, an accelerated growth rate might lead to earlier sexual maturity and thus offspring could be produced faster (Diez et al., 2009). This might help reduce the time required for restocking populations, and therefore be particularly relevant to endangered species.

The problem of an enhanced growth rate may occur in captive individuals of the African spurred tortoise *G. sulcata*. Although this species is widely distributed in Africa south of the Sahara from Senegal to Ethiopia (Loveridge & Williams, 1957; Wermuth & Mertens, 1961; Stearns, 1989; Iverson, 1992), no age-related data on body mass development in free-ranging animals are available. The only age-related data from wild African spurred tortoises are for total length (straight carapace length), given by Hailey & Lambert (2002). Here, we compare these data to data from captive individuals from a private breeding facility to test for differences in growth rates between captive and wild African spurred tortoises.

The African spurred tortoises were kept in outdoor enclosures with natural vegetation of grasses and shrubs during the summer and indoors on hemp in winter. They were fed on fresh grass, wet hay, rarely salad and occasionally vegetables. In their first years of life carp (fish) food was offered as well, as was common practice at the time. The three individuals, two males (A and B) and one female (C), were weighed regularly over a period of almost 18 years.

To test our hypothesis of differing growth rates in captive and wild tortoises, we estimated the growth rates of the three captive individuals studied and compared them with published data for wild individuals. Using data from Hailey & Lambert (2002; read from the graph), we used the individual measurements of age and body mass obtained from different free-ranging individuals as one sample. This generated an average individual (D) of the populations studied in the Sahel by these authors. Due to the fact that for the free-ranging individuals only carapace length measurements were available, whereas only body mass data were available for the captive individuals, we applied the allometric relationship of Lambert (1993; $BM = 0.000922\ L^{2.755}$, BM in grams, L in mm) to each of the length measurements in free-ranging animals. Lambert (1993) showed that this relationship does not significantly

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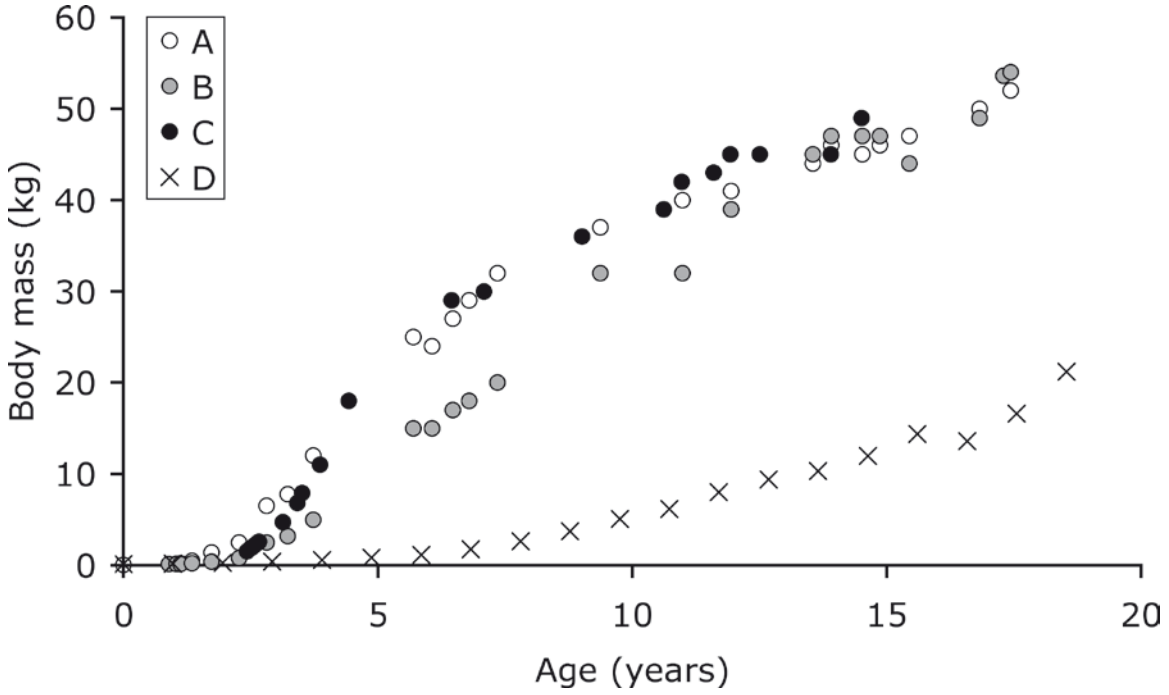

Fig. 1. Relationship of age to body mass development in captive African spurred tortoises (*Geochelone sulcata*) at a private breeding facility (males: A, B; female: C) and in free-ranging animals (D) investigated by Hailey & Lambert (2002). For estimated parameter values of growth models and goodness-of-fit of models, refer to Table 1.

vary between free-ranging and captive African spurred tortoises. The same was observed in leopard tortoises (Ritz et al., 2010).

To find the best growth model for each of the three captive animals and the average wild animal, we considered three mathematical models that relate the mass of an animal *BM(t)* to its age *t*. All models used have been suggested for chelonians (Andrews, 1982; Hailey & Coulson, 1999) and consider an initial body mass BM_0 (in grams), an asymptotic mass BM_∞ (in grams), and the intrinsic growth rate *g* (without units). In particular, we fitted age (in days) versus mass for each individual assuming:

1) the von Bertalanffy growth model:

$$BM\,(t) = (\sqrt[3]{BM_\infty} - (\sqrt[3]{BM_\infty} - \sqrt[3]{BM_0})\,.\,\exp(-gt))^3$$

according to the Pütter–Bertalanffy equation (Pütter 1920, von Bertalanffy 1938, 1957) that allows for non-zero initial body masses (BM_0);

2) the logistic growth model:

$$BM\,(t) = BM_0 + \frac{BM_\infty}{1 + \exp(-g(t - t_i))}$$

where t_i is the age of the individual that corresponds to the inflexion point of the growth curve and defines the age of sexual maturity of the individual according to the resource allocation model (Stearns, 1992). This model is based on the general Chapman–Richards model (Richards, 1959), but assumes a symmetric inflexion point and a non-zero initial body mass;

3) the Gompertz model:

$$BM\,(t) = BM_0 + BM_\infty \exp(-\exp(-g(t - t_{max})))$$

where t_{max} is the age with the maximal increase in body mass (Medawar, 1940). The general Chapman–Richards model (Richards, 1959) reduces to this parameterization of the Gompertz model when an inflexion point close to zero or infinity is assumed.

We applied non-linear regression analysis to estimate parameters of growth models for each of the animals. Analyses were conducted with the software STATISTICA 7.1 (StatSoft, Inc., 2005). Goodness-of-fit was assessed by variance explained (R^2).

There was a distinct difference in the growth of the free-ranging and the captive animals (Fig. 1). The growth in the body mass of each of the captive African spurred tortoises and of the average wild animal was best explained by the logistic model (Table 1). Estimated hatchling masses (BM_0) were, at 0.5–2.0 kg, too high compared to actual hatchling masses of 50–110 g. Asymptotic body mass (BM_∞) was estimated at 51–56 kg in the captive individuals. For the collective free-ranging specimens, BM_∞ was estimated at 27 kg, which is close to the 33 kg estimated for this parameter by Hailey & Lambert (2002) using the original data on an individual basis.

Although for all animals the von Bertalanffy models did converge, the estimated hatchling masses (BM_0) were either strongly negative (e.g. –26kg for individual C) or asymptotic body mass was rather unrealistic (>100kg for B and D) for this growth model. The Gompertz model did not converge for any of the individuals. The intrinsic growth rate (*g*, Table 1) of each of the captive animals was higher than that of the average free-living animal, being 1.4 to 2.6 times higher under the logistic model. Solving the logistic growth equations using the parameters from Table 1 for the year of the highest weight gain (the year that includes the time of the inflexion point), the captive animals had maximum weight gains of 7.7, 5.6

Table 1. Logistic growth models calculated and goodness-of-fit for captive (A, B, C) and free-ranging (D) African spurred tortoises (Hailey & Lambert, 2002). Number of individual measurements (*n*), parameter values derived from non-linear regression analyses (initial body mass BM_0, asymptotic mass BM_∞, intrinsic growth rate *g* [without unit], inflexion point of the growth curve t_i = age in days that corresponds to sexual maturity), and variance explained (R^2); * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

			Parameter estimates				Goodness-of-fit
Animal	Sex	*n*	BM_0 (g)	BM_∞ (g)	*g*	t_i (days)	R^2
A	Male	25	1546**	53546**	0.001617***	2174***	0.95
B	Male	25	1659**	55632*	0.001112***	3173***	0.98
C	Female	22	2020*	51020*	0.002080*	2156*	0.96
D	Unknown	20	460*	26891**	0.000788***	5604***	0.99

and 9.4 kg per year, respectively, compared to 1.9 kg per year for the free-ranging animals.

Assuming the resource allocation model (Stearns, 1992), in which sexual maturity coincides with the inflexion point of the growth curve where growth rate decelerates, the logistic model predicted that captive male A reached sexual maturity at an age of about 6.0 years, captive male B at an age of about 8.7 years and captive female C at an age of about 5.9 years (Table 1). It was observed that both males masturbated at between four and five years old (as confirmed by microscopic identification of ejaculate) and that the female laid her first eggs at the age of five years. In contrast, the estimated age of sexual maturity was 15 years (inflexion point) for free-ranging animals.

The results confirm observations in other tortoise species that captive individuals display faster growth than their free-ranging conspecifics. This is most likely due to intensive feeding under captive conditions; it should, however, be noted that this does not automatically imply a nutrient-imbalanced or a nutrient-deficient diet, but can also be the result of a balanced diet offered in high amounts (Furrer et al., 2004; Diez et al., 2009; Ritz et al., 2010).

Our analysis of growth curves of animals revealed that the logistic growth model best described growth in body mass of African spurred tortoises. The Gompertz model and the von Bertalanffy model were not applicable, because the first did not converge and the second revealed biologically unrealistic estimates of growth parameters. Hailey & Lambert (2002) also found in their analysis of four African spurred tortoises that the logistic model fitted the growth of three individuals best, and that the Gompertz model was appropriate for one individual only. The von Bertalanffy model, which is generally suggested for reptiles (Halliday & Verrell, 1988), did not yield applicable results either in this study or in the study by Hailey & Lambert (2002). These observations question the generality of the von Bertalanffy model for reptiles (Halliday & Verrell, 1988) but support the observations of Avery (1994) that mass growth in smaller reptiles and chelonians is best fitted by a logistic model (Chen & Lue, 2002). Further support for the applicability of the logistic model to African spurred tortoises comes from accuracy of estimated ages at sexual maturity. The captive female tortoise laid her first eggs at the age of five years, which is close to the age of about 5.9 years predicted by the logistic model. We did not observe the first copulation of males, but noticed that they masturbated at an age between four and five years. However, the discrepancy between the estimated and the actual hatchling mass indicates that even the logistic model is not ideal.

Based on the growth-curve-based estimates of sexual maturity, we suggest that faster growing tortoises reach sexual maturity earlier than slower growing individuals, and that generation times in restocking programmes could be distinctly reduced if breeding animals were raised intensively. In the literature for private tortoise breeders, one may find warnings against fast growth, and even warnings that offspring of faster growing animals may be less viable (e.g. Wegehaupt, 2006). To our knowledge, further evidence for these claims is lacking in tortoises, and one might suspect that such effects may be more evident if fast growth is triggered by high amounts of an inappropriate diet rather than by high amounts of an appropriate diet. However, reports that home-bred *Testudo* hatchlings had lower survivorship than hatchlings from free-ranging populations (Lambert et al., 1988), and that faster-growing individual lizards and skinks have lower survival rates in the wild (Bradshaw, 1970, 1971; Olsson & Shine, 2002), indicate that for restocking programmes, it seems prudent to ensure that the generation intended for release in the wild is maintained for a long period, with slow growth. Whether the quality of offspring itself is influenced by the growth rate of the parent animals remains to be investigated.

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Accepted: 9 June 2010

Artikel 3

Variation in growth and potentially associated health status in Hermann's and Spur-thighed tortoise (*Testudo hermanni* and *Testudo graeca*)

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Abstract
Captive reptiles often show higher growth rates than in the wild, possibly due to higher feeding intensity. Although health problems are usually linked to inappropriate diets, fast growth itself, such as triggered by appropriate diets fed in high amounts, has traditionally also been considered unfavourable for tortoises. We document growth rates (based on age and mass) from private *Testudo hermanni* and *graeca* breeders, which are generally higher than those reported for free-ranging specimens, but show enormous variation. Tortoise patients presented to an exotics clinic also covered the whole growth rate spectrum. To test whether fast growth was associated with diseases, the age-body mass relationship of these patients was tested, in a retrospective evaluation, for additional influence factors, such as dietary history and occurrence of certain diet and growth-related diseases. No indication was found that animals particularly heavy for their age were more prone to diet/growth related disorders. In general, tortoises fed diets with meat/grain were heavier for their age than tortoises fed more appropriate diets; dietary history was not related to a particular disease. The results suggest the age-body mass relationship may not be suitable for testing effects of fast growth; an age-body length relationship would be more appropriate. Animals presented for a diet/growth related disorder were younger than animals presented for other reasons; there was a significant negative correlation between the severity of pyramiding and age, suggesting that growth-related disorders may well limit the life expectancy of tortoises. Controlled clinical studies are required to fully test this hypothesis.
Key words: diet, pyramiding, reptile, herbivory

Introduction
Intensively kept tortoises show growth rates that exceed that of extensively kept or free-ranging animals (Lambert, 1982 - *Testudo graeca*; Lambert et al., 1988 - *T. graeca, T. hermanni, T. marginata*; Zwart et al., 1997 - *T. hermanni*; Furrer et al., 2004 - *Geochelone nigra*; Lapid et al., 2005 - *T. graeca*; Ritz et al., 2010a - *G. sulcata*; Ritz et al., 2010b - *G. pardalis*). Although experimental evidence is mostly lacking, the main cause for the growth discrepancy between captive and free-ranging tortoises is probably the difference in diet, but other factors might also be involved (Andrews, 1982). Amongst these are humidity (Wiesner and Iben, 2003), individual temperature optimum (Avery et al., 1993; Adolph and Porter, 1996; Wegehaupt, 2006), availability of drinking water (Lorenzon et al., 1999), and ultraviolet light or Vitamin D supplementation (Heuberger, 2008). Differences in the load of gastrointestinal parasites, other parasites, typhlocolitis due to different reasons or renal diseases may also influence the tortoise's development, especially the constitution of the carapace due to impaired calcium absorption (Häfeli and Zwart, 2000). Different factors that influence the activity level of a reptile could influence the growth rate as well. Lorenzon et al.'s (1999) results on insectivorous common lizards (*Lacerta vivipara*) showed that a low activity level is associated with a low growth rate. Two theories are discussed for that phenomenon: Firstly, the activity level is

directly related to the time spent in a preferred temperature zone and therefore to the time when physiological processes (as food digestion and resulting metabolism and growth) are most efficient; and secondarily, less active lizards spend less time preying and hence have a lower food intake.

To our knowledge, the only studies providing evidence for an effect of different food compositions on growth in herbivorous tortoises are the ones by Wiesner and Iben (2003), Fledelius et al. (2005) and Diez et al. (2009). Wiesner and Iben (2003) showed that *Geochelone sulcata* fed a complete diet with low protein content tended to show less pyramiding than animals on a high-protein diet (but note that humidity was the major factor influencing pyramiding in that study); these findings corroborate the experience of Stearns (1989) that a high-protein diet led to more pyramiding than a low-protein diet (but that the low-protein diet alone did not prevent pyramiding completely). Fledelius et al. (2005) examined the influence of calcium supplementation on the growth rate of *Geochelone pardalis*, and the individuals receiving a calcium dose three times higher than recommended showed the highest growth rate. Diez et al. (2009) observed that tortoises that received a high amount of a herb diet grew faster than individuals fed the same diet at restricted amounts. Whether animals underwent hibernation or not also influenced growth in that study, as non-hibernating animals continued to eat and grow during the winter period.

Nevertheless, controlled, experimental studies on the influence of feeds used in captive situations in zoos or by private breeders are mostly lacking – probably due to the long time periods necessary for such experiments. Recommendations to feed tortoises sparingly and with high-fibre diet items are derived from observations on the natural diet (e.g. Lagarde et al., 2003; El Mouden et al., 2006), anecdotal observations of captive animals (e.g. Stearns, 1989), and common sense. Before making quick judgements on pet owners who feed cat food to their herbivorous tortoises, we should remember that historically, the use of diets with animal protein was common and even recommended (see Table 1), that a cat-food based diet has even been recommended recently for fast growth in herbivorous tortoises without mention of potential side-effects (Lapid et al., 2005), and that general recommendations to exclude such items (Calvert, 2004b; McArthur and Barrows, 2004; Donoghue, 2006; Wegehaupt, 2006) are comparatively recent.

With respect to tortoise diets, two different factors need to be considered separately that may, in practice, often occur in parallel: an inadequate diet composition (in terms of diet items and nutrients; in particular high-protein diets due to the use of meat products; calcium deficiency), and a high amount of food offered. In particular, the consequences of feeding a high amount of food will vary between an adequate or an inadequate diet. For example, the captive tortoises investigated by Stearns et al. (1989), Furrer et al. (2004) and Ritz et al. (2010a; 2010b) either did not receive any animal protein or only, in the case of *Geochelone sulcata* (Ritz et al., 2010a), at the very beginning of their lives, but nevertheless all showed growth rates exceeding that of free-ranging animals. Hence, it seems possible that even plant food may trigger fast growth in tortoises, especially when offered ad libitum (Diez et al., 2009). This fast growth, if triggered by high amounts of an adequate diet, must not necessarily be linked to conditions associated with an inadequate diet. For example, Donoghue (2006) suggests that overfeeding per se does not lead to the malformation of the carapace usually termed ‘pyramiding’, but that nutrient imbalances are responsible for this. An inadequate diet, in contrast, is also often associated with increased growth (because such diets are usually high in energy and protein, feeding them mostly automatically leads to excessive supply),

but also with pyramiding (also not as the only reason), bone malformation, or gout (Calvert, 2004b; Donoghue, 2006; Wegehaupt, 2006; Hatt, 2008).

The assumption that fast-growing tortoises show pyramiding growth of the carapace is common, but the consequence of this shell abnormality on the health status of the tortoises has not been investigated systematically. Wegehaupt (2006) distinguishes pyramiding *with an abnormal bone structure underneath the scutes* from pyramiding *without an abnormal bone structure*. He observed that free-ranging tortoises living in arid zones with limited water access often show pyramiding with a normal bone structure, whereas individuals of the same species from habitats with higher environmental moisture develop a smooth carapace. Lambert (1982) also noted that free-ranging *Testudo graeca* living in arid regions showed uneven carapace scutes compared to individuals from more humid regions. Abnormalities in the bone structure of the carapace, however, are ascribed by Wegehaupt (2006) to an intensive feeding with a high-protein diet. He suggests that the result is a porous and thickened carapace, as is often observed in tortoises kept as pets (Lambert et al., 1988). Again, data backing these claims are missing.

Faster-growing individuals reach sexual maturity earlier (Jackson et al., 1976; Jackson et al., 1978; Lambert et al., 1988; Ritz et al., 2010a), which could help saving years in restocking programs of highly endangered land tortoise species (Aresco and Guyer, 1999; Ritz et al., 2010a). Pees et al. (2010) suggest that intensive feeding might trigger an early sexual maturation and egg production for which the body is 'not yet prepared'. Again, data or references that back these claims are missing. If a faster growth leads to an earlier sexual maturity, problems should only occur if reproductive activity occurs disproportionately early in faster-growing individuals. Evidence for this is, to our knowledge, lacking so far. Fast growth is also traditionally associated with other health problems in the literature on tortoise husbandry, leading to higher mortality and also reduced lifespans (Furrer et al., 2004; McArthur and Barrows, 2004; Wegehaupt, 2006). In the opinion of Wegehaupt (2006), offspring of fast-growing individuals may be infertile already in the second generation; these claims are, however, not backed by data.

We investigated historical records of tortoises presented as patients to our clinic in order to test for potential evidence that individuals for which a fast growth can be suspected were particularly prone to disease, and whether associations between fast growth and husbandry information provided by owners could be detected. In addition, we also surveyed private tortoise breeders for growth records of their animals.

Methods

Private owners of *Testudo hermanni* and *Testudo graeca* were contacted by an appeal in TESTUDO, the journal of the community of interest in tortoises and turtles in Switzerland (Schildkröten-Interessengemeinschaft Schweiz, SIGS) to collect data on the age and body mass of their animals. Only data from tortoises were used that were, in the opinion of their owners, free of health problems. Data for 65 *Testudo hermanni* of 11 different owners and data of 21 *Testudo graeca* of 6 owners were available. Comparative data was also collected from the literature (Kirsche, 1971; Lapid et al., 2005; Wegehaupt, 2006).

Case histories of the years 2000-2009 from the archive of the Clinic of Zoo Animals, Exotic Pets and Wildlife of the Vetsuisse Faculty of the University of Zurich were evaluated. Only cases were selected where the owner had provided an age of the animal. This information had to be taken at face value; individual cases where the veterinarian on duty had made a note that the age information appeared questionable (by adding a question mark on the medical history sheet) were not

included in the analysis. Animals had been weighed as part of the routine clinical examination.

Data on the age, body mass, sex, feeding history and health problems were available for 539 animals of *Testudo hermanni*, *Testudo graeca* and tortoises of unknown species (but, most likely, of either one). Age was recorded in days and the body mass in grams. The information on the diet given by the owner was qualitative (i.e. no proportions or quantities were given); this information was used to classify animals into three diet categories: (1) animals were only fed extensively with hay, grass, herbs and salad; (2) animals received in addition vegetables, fruits and/or pellets; (3) animals were fed intensively with meat and/or grain products.

In reptile medicine, various types of 'metabolic bone disease' have been described (Mader, 2006). In the clinical reports, the terms 'metabolic bone disease', 'pyramiding' and 'fibrous osteodystrophia' were the most prominent ones that might have been used, by the various veterinarians, to describe a similar problem. In order to preserve the original data structure, we included both the note 'metabolic bone disease' (presumably a finding mainly based on history, radiographs, palpation, and supported by blood mineral analysis) and 'pyramiding' (presumably based on a visual impression) among the health problems of the animals that were included in this study. These two observations were included, together with the less frequently noted categories of obesity, renal problems (suggesting gout), and fibrous osteodystrophia, in the general category of "dietary/growth disorders".

Further information was collected on parasite occurrence in the faeces, whether or not the owner allowed the animal to hibernate, and the outcome of the visit to the Clinic (treated and returned home, or euthanized/died during treatment). If latero-lateral radiographs were available in the archive, the status of carapace deformities was noted. On the one hand, a 5-step categorical classification was used (ranging from 0=no pyramiding to 4=extreme pyramiding); on the other hand, pyramiding was quantified as a ratio of measurements. On the radiographs, the distance between centres of the third and the fourth central scutes and the depth between the humps of these two scutes was measured (Fig. 1). The ratio of the depth to the distance was then used as measurement of the extent of the carapace deformation. The correlation between the categories and the quotient was highly significant (Spearman's $R=0.865$, $p<0.001$).

Data on age and body mass were ln-transformed prior to further analyses. The effects of various factors on the fundamental relationship between age and body mass were evaluated by General Linear Models. Because not all data were available for all animals, sample size n varied between different analyses. Interaction terms between factors and measurements were included in the GLMs when appropriate. Correlations were tested using nonparametric tests if data were not normally distributed. The influence of a categorical variable (e.g. hibernation, diet, parasite status) on other categorical variables (e.g. disease status) was tested by chi-square tests. The significance level was set at 0.05. All tests were performed in PASW 18.0 (SPSS Inc., Chicago, IL).

Results

The evaluation of the growth data of *T. hermanni* and *T. graeca* kept by private owners in Switzerland showed a broad range of body mass development, although only data from individuals without obvious health problems were investigated (Fig. 2a and b). Available data from the literature on free-ranging or extensively-kept animals fell within the range observed in private breeders, indicating that at least some breeders actually provided conditions that mimicked the natural habitat in their effects on growth (Fig. 2c and d); however, in general it seemed that free-ranging animals were at the lower part of the range, especially in *T. graeca* (Fig. 2d). Date

from *T. graeca* kept on cat food from Lapid et al. (2005) showed a faster growth rate than that achieved by most breeders (Fig. 2d).

When the data from apparently healthy animals was compared to that of animals presented as patients to our clinic, it is evident that most patients fell into the same growth range, with some outliers (Fig. 2e and f). In particular, the *T. hermanni* patients appeared to be divided into old animals that were comparatively heavy, and those that were comparatively light for their age (Fig. 2e).

The relationship between age and body mass was highly significant (n=539, $F_{1,537}$=1247.122, p<0.001). Species (*T. hermanni* or *T. graeca*) did not affect this relationship significantly (n=147, overall model: $F_{2,144}$=254.378, p<0.001; cofactor species $F_{1,144}$=0.061, p=0.805); subsequent analyses, therefore, do not differentiate between the species. Instead, both sex (male/female) and the sex-age interaction were significant (n=348, overall model $F_{3,344}$=145.220, p<0.001; cofactor sex $F_{1,344}$=9.911, p=0.002; sex-age-interaction $F_{1,344}$=12.983, p<0.001) – in the dataset, younger males were heavier, and older males were lighter, than similar-aged females (Fig. 3a). Whether animals were made to hibernate or not did not affect the age-mass relationship (n=211, overall model $F_{2,208}$=222.841, p<0.001; cofactor hibernation $F_{1,208}$=0.002, p=0.964). The effect of diet (categories 1-3) on the age-mass relationship was significant (n=416, overall model $F_{3,412}$=402.722, p<0.001; cofactor diet $F_{2,412}$=3.566, p=0.029), with animals from diet category 3 (intensive feeding) having slightly higher body masses for their age. If diet categories 1 and 2 were combined and compared only against diet category 3, the difference was even clearer (n=416, overall model $F_{2,413}$=265.240, p<0.001; cofactor diet $F_{1,413}$=5.422, p=0.020). Note that the difference was, however, even if significant, not particularly pronounced (Fig. 3b). Whether animals had parasites also had a significant effect on their age-specific body mass (n=150, overall model $F_{2,147}$=158.621, p<0.001; cofactor parasites $F_{1,147}$=6.325, p=0.013) (Fig. 3c). The presence of diet/growth disorders in general ($F_{1,536}$=2.167, p=0.142), pyramiding deformations ($F_{1,536}$=0.033, p=0.856), metabolic bone disease ($F_{1,536}$=3.028, p=0.082), or both ($F_{1,536}$=1.091, p=0.297), did not have a significant effect (Fig. 3d). Among females, animals with dystocia did not differ from other animals (n=177, overall model $F_{2,174}$=129.052, p<0.001; cofactor dystocia $F_{1,174}$=1.092, p=0.297). The pyramiding category (based on the x-rays) had a significant effect (n=75, overall model $F_{5,68}$=39.100, p<0.001; cofactor pyramiding category $F_{4,68}$=2.561, p=0.046), and the pyramiding quotient (based on the x-rays) was close to being a significant covariable (n=75, overall model $F_{2,72}$=90.545, p<0.001; covariable pyramiding quotient $F_{1,72}$=3.401, p=0.069). Pair-wise comparisons using Sidak adjustement for multiple testing, however, did not reveal any significant difference in the age-mass relationship between the five pyramiding categories (Fig. 3e). Whether animals left the clinic alive, or died/were euthanized had a significant effect on their age-specific body mass (n=536, overall model $F_{2,533}$=620.845, p<0.001; cofactor ending $F_{1,533}$=4.097, p=0.043), with surviving animals generally having a higher body mass (Fig. 3f).

Animals that received a diet comprising meat/grain (diet category 3; n=38; 3776 ± 3 d) were, on average, older than animals not receiving these items (diet category 1+2; n=380; 2239 ± 4 d) (t-test of ln-transformed age, p=0.021); there was, however, no age difference between animals receiving diet category 1 and diet category 2 (p=0.857). Animals with diet/growth disorders in general were, on average, younger (n=272; median 2190, range 122-36500 d) than animals without such problems (n=267; 2555 d, 30-29200 d) (U-test, p=0.016). The same was the case for animals with (n=38; 1095 d, 244-36500 d) or without metabolic bone

disease (n=501; 2555 d, 30-36500 d; U-test, $p<0.001$), and for animals with (n=123; 1095 d, 122-27375 d) and without pyramiding (n=416; 3285 d, 30-36500 d; U-test, $p<0.001$). There was a negative correlation between the pyramiding quotient and age (n=75, Spearman's R=-0.243, p=0.035), indicating that particularly pronounced cases of pyramiding were mainly seen in younger tortoises.

Using the chi-square test, there was no evident risk, for any disease, outcome or husbandry factor linked to sex. Neither whether animals were allowed to hibernate, or whether they had parasites, was linked to any other disease, outcome or husbandry factor, with the only exception that animals that received diet categories 1+2 had parasites significantly less frequently (14 out of 110 cases) than animals that received diet category 3 (4 out of 10; p=0.021). There was no evident risk due to diet categories 1+2 vs. category 3 for diet/growth disorders (p=0.783) or pyramiding deformations (p=0.795). There was no single case of metabolic bone disease in animals receiving diet category 3; all cases of MBD occurred in animals on diet categories 1+2 (chi-square p=0.050). Diet did not relate with whether animals survived or died/were euthanized (p=0.484).

Discussion

The results of this study underline the high degree of phenotypic flexibility in herbivorous tortoises with respect to growth. This is evident from comparisons between animals raised under different conditions, both between the wild and captivity, between intensive and extensive husbandry systems, between breeders and between animals kept at the same breeder (Fig. 2a-d). While differences between the wild and captivity, and between different husbandry regimes, may well be mainly due to differences in diet composition and amounts of diets offered (for other reasons see Introduction), the findings also suggest that under one husbandry regime, individual differences in growth can occur that are less easily explained. Dickinson (1985) and Lambert et al. (1988) already remarked that the growth development of tortoises between and within clutches differs remarkably even if the animals were kept under the same conditions.

The results from the analyses of our clinic's patients are less clear-cut. Evidently, the major limitation of a survey like this one is the absence of data for the control group – those animals kept by private owners that are considered healthy and not presented for examination and treatment. Additionally, a retrospective evaluation like this one necessarily lumps not only information by various owners but also measurements and diagnoses made by various veterinarians; the data will therefore contain a large margin of inconsistency.

Both *T. hermanni* and *T. graeca* are species known for their sexual dimorphism, with females attaining larger body masses than males (Willemsen and Hailey, 2003) – a pattern also reflected in the patients of this study (Fig. 3a). Interpretations on the associations of body mass with other factors are difficult to translate into conclusions about husbandry and disease in tortoises. On the one hand, a comparatively lower body mass was associated with parasite infestation (Fig. 3c) and a fatal condition (Fig. 3f), which suggests that parasite infestations and or any other condition related to a fatal outcome were mainly chronical conditions, which led to reduced body masses. The finding that conditions summarized as 'diet/growth disorders' were not associated with body masses that were high for the animals' age can, in this respect, not contradict the idea that high growth rates can lead to disease in tortoises, but rather suggest that in order to thoroughly collect evidence for the damaging impact of high growth rates, carapace measurements rather than weighing of animals are required. If any condition of the animal leads to chronic illness, body mass will decrease (Jackson, 1980) – which means

that, in our retrospective study that focuses on the age-body mass relationship, animals suffering from intensive diets and/or fast growth cannot be properly identified. Carapace length measurements would allow a doubtless identification of animals with high growth rates, and deviation from the typical carapace length-body mass relationship would additionally indicate animals with chronic weight loss (Jackson, 1980). Therefore, while this study cannot provide evidence for negative effects of fast growth on tortoise health, future data collections should focus on collecting age, body mass and body length information together as routine measurements/questions in the clinical investigation of tortoises.

In this retrospective analysis, diet could only be evaluated in terms of its composition, but not in terms of amounts fed. Although animals receiving diet category 3 (incl. meat/grain products) had significantly higher mean body masses for their age, they were well within the range observed in tortoises fed either diet category 1 (hay, grass, herbs, green vegetables) or 2 (incl. fruits, vegetables, pellets). Diet category did not relate with growth diseases or pyramiding – in this respect, qualitative dietary information is probably not sufficient to evaluate a correlation. Rosskopf and Shindo (2003) also commented anecdotally that an evident relationship between the dietary history of animals and their shell health is not always evident. Diet category 3 was predominantly used in older animals, which suggests that the historical development outlined in Table 1 is mirrored in the fact that owners keeping animals since more recent times avoid meat/grain products in general. The relationship between diet 3 and the presence of parasites, even though based on a small sample size, could also indicate that owners feeding diet 3 are generally less informed or concerned about their tortoises' health. However, the findings also indicate that feeding fruits and non-green vegetables is still common practice, although it is generally discouraged in scientific texts (Calvert, 2004b; McArthur and Barrows, 2004; Donoghue, 2006; Wegehaupt, 2006). To prove direct effects of diet on growth, pyramiding, disease and survival in tortoises, long-term feeding experiments are required.

While our retrospective study cannot provide direct evidence for a correlation of growth rates with growth diseases, including metabolic bone disease or pyramiding, or of the presence of pyramiding with disease and survival, the age distribution of patients suffering from these growth diseases represents some indirect evidence. These problems were significantly more frequent in younger than in older tortoises; in the case of quantitative pyramiding data, there was even a negative relationship between the severity of pyramiding and age, indicating that more severe cases occur in younger animals. It is known that growth diseases such as metabolic bone disease predominantly affect younger animals (Mader, 2006). The scarcity or absence of older animals in this disease group suggests that health problems either dissolve (with or without treatment), or that these health problems lead to a low survival, so that animals with these health problems appear in older age classes less frequently. Especially in the case of pyramiding, dissolution of the condition appears unlikely, and the results of this study thus could suggest that pyramiding in pet tortoises indeed reduces their longevity. However, in the absence of controlled studies, these interpretations remain speculative.

The question whether inappropriate amounts and/or an inappropriate composition of the diet causes malformation, disease and low survival in tortoises remains unanswered. However, even in the absence of evidence gained from controlled studies, husbandry practices should be followed that appear logical, when compared to the conditions the animals live under in the wild, and in consideration of the anatomy and

physiology of their digestive tract. For future studies, the documentation of not only age and body mass, but of carapace length and ideally the pyramiding quotient (measured easily in live animals) is recommended in tortoises presented to veterinary consultation.

Conclusions

1. Tortoises show great plasticity in growth rates, which are often linked to intensive feeding (of both appropriate or inappropriate diets).
2. The relationship between age and body mass did not indicate a particular susceptibility of relatively heavier animals presented to an exotics clinic for diet or growth related disorders.
3. This may be due to the chronic nature of disease processes in tortoises, which are often linked to weight loss. For a proper evaluation of an increased susceptibility of relatively fast-grown individuals to certain diseases, carapace length measurements should be recorded routinely in tortoise patients.
4. Growth-related disorders, in particular pyramiding, occurred more frequently in younger tortoise patients. This might indicate that such conditions limit the life expectancy of the tortoises, but cannot be considered conclusive evidence.
5. To correctly assess the health risks related to fast growth (as triggered by high amounts of an appropriate diet) in tortoises, controlled clinical studies are required.

Acknowledgements

We thank the anonymous tortoise breeders for sharing their data on age and body mass of their animals; in the Clinic for Zoo Animals, Exotic Pets and Widlife of the Vetsuiss Faculty, University of Zurich, we thank the treating veterinarians of the last decade, as well as our animal care team, for recording the animals' conditions.

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Table 1 Recommendations from sequential issues of a standard textbook for the feeding of herbivorous tortoises; note that these information are not intended as actual recommendation but as an example how feeding recommendations for tortoises changed historically. With respect to the most recent recommendations, note that other textbooks (e.g. Calvert, 2004a; Donoghue, 2006) do not recommend dog or cat food, milk products or grains at all.

Year	Recommendation	Source
1980-1993	80% fruits, 19% meat, 1% minerals; fruit: apple, pear, orange, banana, tomato, greens (fresh grass, clover, salad); meat: muscle, heart – cut to fine pieces – also complete feeds for dogs and cats. If fruit is scarce: oat flakes, rice, dry dog food, steamed potatoes	(Meyer et al., 1980; Meyer et al., 1989; Meyer et al., 1993)
1999	Leafy greens, vegetables, fruit (apple, banana, pear, grapes, kiwi), sometimes moist dog and cat food, grain products	(Kamphues et al., 1999)
2004-2009	Greens (wild herbs and a small proportion of salad and vegetables), small amounts of fruits (may lead to malfermentation and diarrhoea), moist dog and cat foods should not be a major component (cause gout), milk and grain products only in limited amounts, hay always ad libitum, sepia or egg shells as calcium sources	(Kamphues et al., 2004; Kamphues et al., 2009)

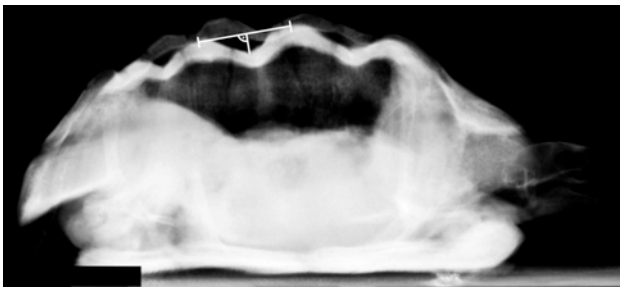

Figure 1 Quantification of the hump formation of the carapax of herbivouros tortoises (*Testudo* spp.) on laterolateral radiographs.

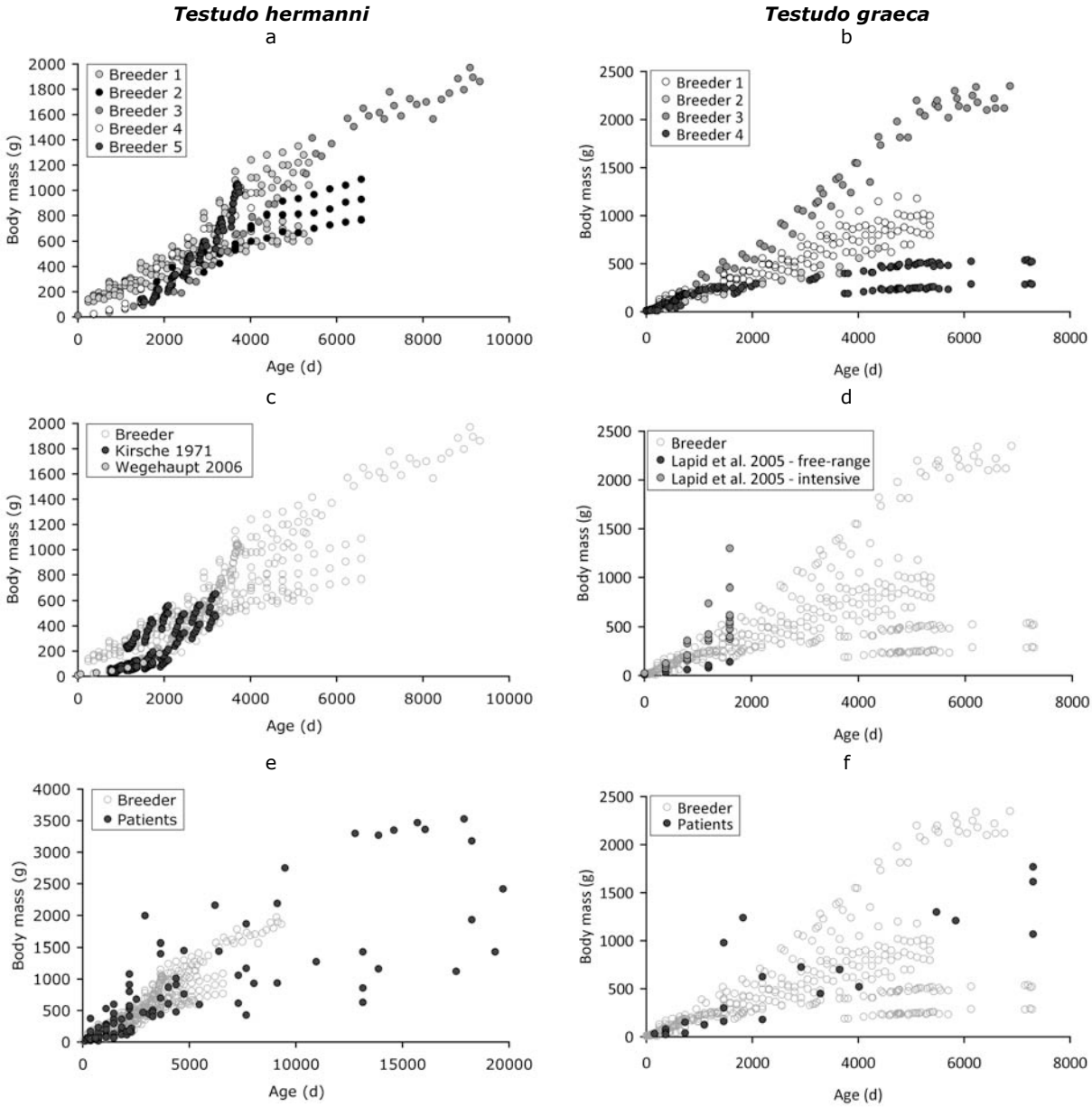

Figure 2. Relationship between age and body mass in *Testudo hermanni* and *Testudo gaeca* from private breeders (a,b), compared to data from free-ranging, extensively kept or intensively kept individuals (c,d), and compared to the data for the tortoise patients of this study.

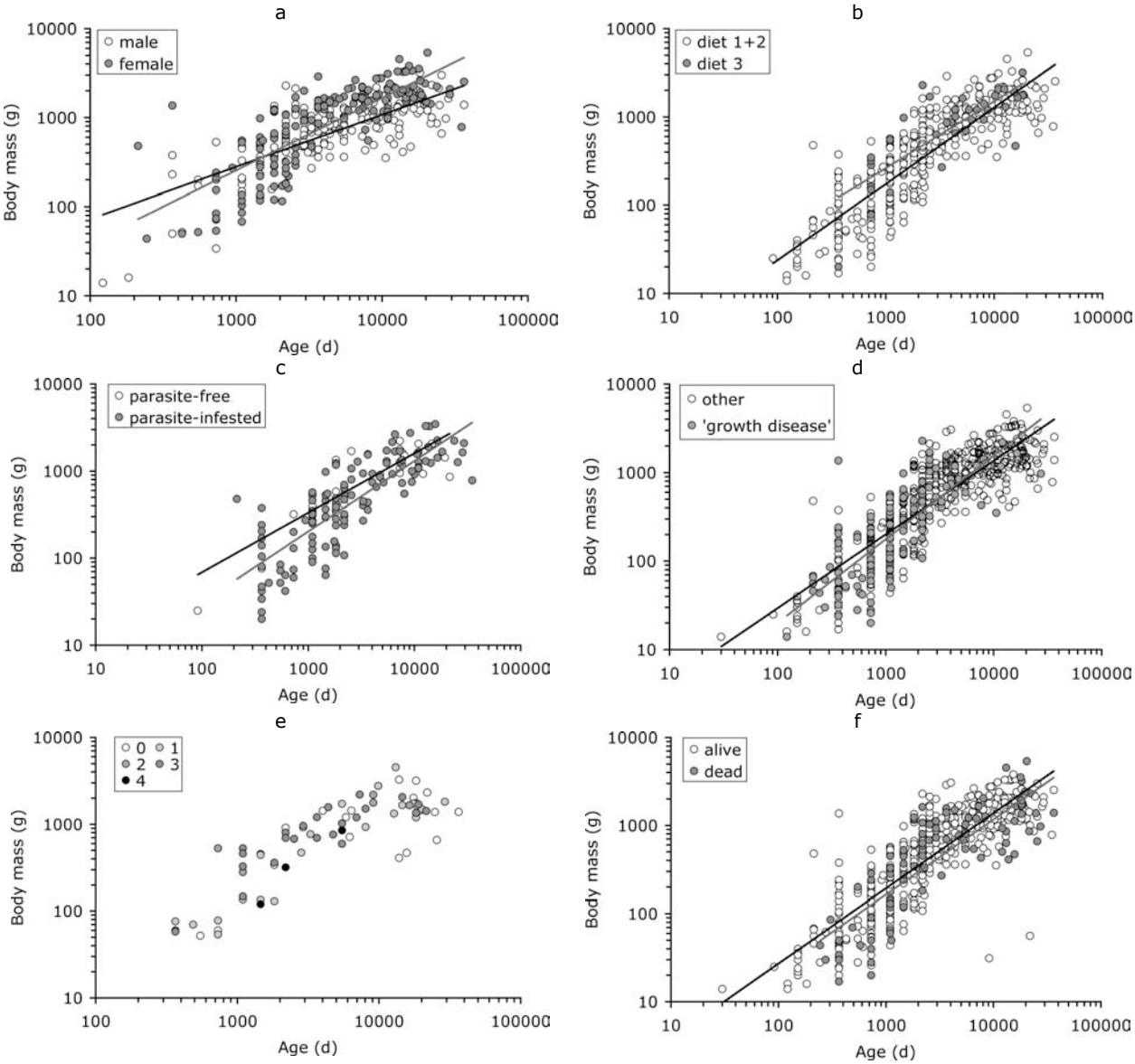

Figure 3. Relationship between age and body mass in the tortoise patients of this study, as separated by a) sex, b) diet, c) parasite status, d) the presence of the 'diet/growth disorders' complex or other reasons for presentation as patients, e) the degree of pyramiding (from 0=absent to 4=extreme), f) whether the patient survived or not.

Danksagung/Acknowledgements

This dissertation would not have been possible without the help of many people:

I thank Prof. Dr. Jean-Michel Hatt for the opportunity offered in the form of the participation in the "Zoo Research Camp", and for offering the chance to pursue this topic further beyond, including the work on the stored datafiles of the Clinic for Zoo Animals, Exotic Pets and Wildlife.

I thank my supervisor, PD Dr. Marcus Clauss, for his engaged support during all the different steps of this dissertation.

I would like to thank Sheikh Saoud bin Mohammed bin Ali Al-Thani, the owner of the Al Wabra Wildlife preservation (AWWP), Dr. Sven and Catrin Hammer and the stuff of AWWP for giving me the opportunity to use the data they have collected during many years and to collect additional data myself.

Many thanks go to Ruth Huber and all the other private tortoise breeders who provided me their data and to my co-authors E. M. Griebeler from the Institut of Zoology from the Johannes Gutenberg University in Mainz, Germany and W. J. Streich from the Leibniz Institute of Zoo and Wildlife Research (IZW) in Berlin, Germany.

Last but not least I thank my family and boyfriend for their support and patience.

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